NSL 64-29-6

PROGRESS REPORT

INVESTIGATION OF PEROGNATHUS AS AN EXPERIMENTAL ORGANISM FOR RESEARCH IN SPACE BIOLOGY

1 January through 31 March 1965

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PREPARED UNDER CONTRACT NASw-812

for

OFFICE OF SPACE SCIENCES
NATIONAL AERONAUTICS AND SPACE ADMINISTRATION
WASHINGTON 25, D.C. 20546

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REPRODUCTION OF PEROGNATHUS IN CAPTIVITY

P. Hayden, J. J. Gambino
and R. G. Lindberg

INTRODUCTION

Use of Perognathus as an experimental tool would be greatly enhanced by having available large numbers of laboratory-reared animals from a genetically known breeding colony. Not only would this provide a more stable population for experimental purposes, but also, it would obviate dependence upon exigencies of field collecting.

Unfortunately, breeding by other investigators of captive heteromyid rodents, including Perognathus, Dipodomys, and Liomys, has had only marginal success (1,3,6,7). Results of this work was summarized in an annotated bibliography included in an earlier report to NASA*.

The only species of Perognathus which appear in the literature as having been successfully bred in captivity are P. californicus and P. flavus (7). Because of the extreme aggressiveness of Perognathus, these matings were accomplished only by very carefully controlling environmental conditions and pairing methods. For example, size of the mating pens and time period of contact between the sexes appeared to be extremely important. In addition, precise estimates as to when the female might be most receptive was most essential.

Dipodomys appears somewhat easier to breed than Perognathus. This conclusion is based on the availability of at least four separate reports of successful laboratory breeding of various species of Dipodomys (1,3,6,7). As in Perognathus, behavior patterns of Dipodomys, which reflect the

* Final Report NSL 62-125-5, Contract NASr-91, Submitted to NASA, Aug. 1963

solitary habit and strong territorialism of these heteromyids, present the greatest obstacles to laboratory matings. Apparently, aggressiveness is not as pronounced in some species of Dipodomys as it is in Perognathus. With Dipodomys, as with Liomys and Perognathus, successful breeding depends upon drastic modification of the usual breeding techniques employed for breeding laboratory animals (6). This conclusion appears to be unanimous among those who have ever attempted to breed heteromyids in captivity.

Efforts to breed Perognathus in this laboratory were directed along the lines suggested from the literature. After repeated failure to obtain breeding animals by these methods, a systematic approach was adapted involving field observation, observation of natural breeding cycles in captive animals, and induced breeding cycles in captive animals. This interim communication notes our progress to date.

REPRODUCTIVE CYCLES

Estrous Cycle

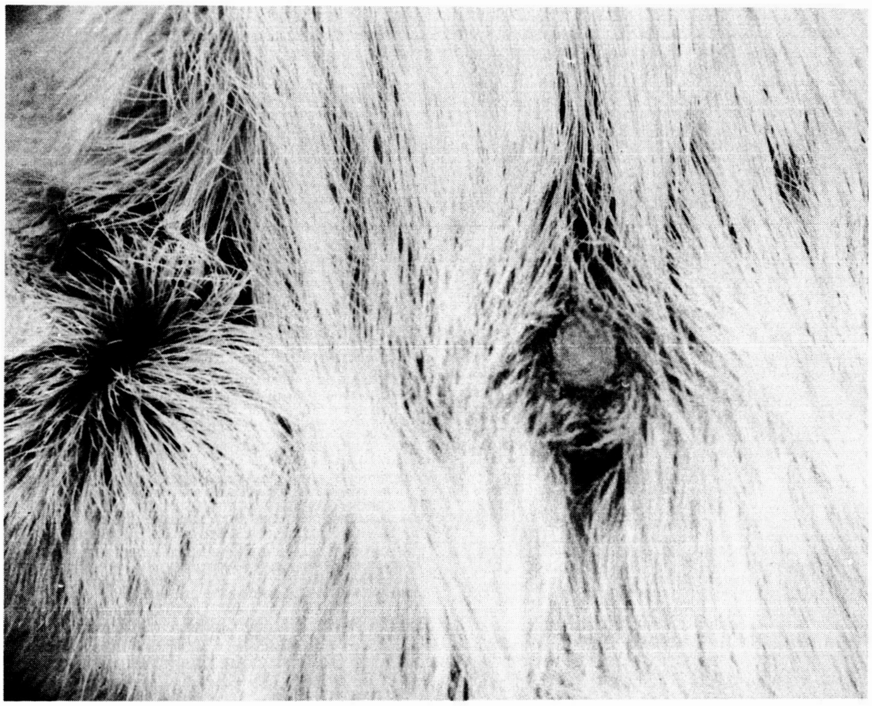
The polyestrous cycle of *P. longimembris* starts about mid-January in the laboratory. An estrous cycle is completed in about 10 days. Two or more estrous cycles have been observed in some individuals, while others have shown only one cycle.

The vaginal orifice is completely regressed and tightly sealed with epithelial tissue during the anestrus portion of the yearly cycle (Plate I-A). During the polyestrous cycle period the orifice is alternately open and lightly sealed (or lips tightly oppressed). The first sign of the estrous cycle is vulval swelling which occurs during proestrus, 1 - 2 days before estrus (Plate I-B). The vaginal lips remain sealed during proestrus, but a characteristic horizontal line is evident. During the receptive period, estrus, the vaginal orifice is open, with the lips of the vagina much enlarged and evaginated to various degrees (Plate II-A). This condition may last a day, but sometimes lasts just a few hours. During metestrus, the external genitalia regresses and increased cornification and sloughing of the vaginal lining occurs (Plate II-B). The lining is much crenulated and eventually consolidated into a central core which is retained in the animal from one to five days.

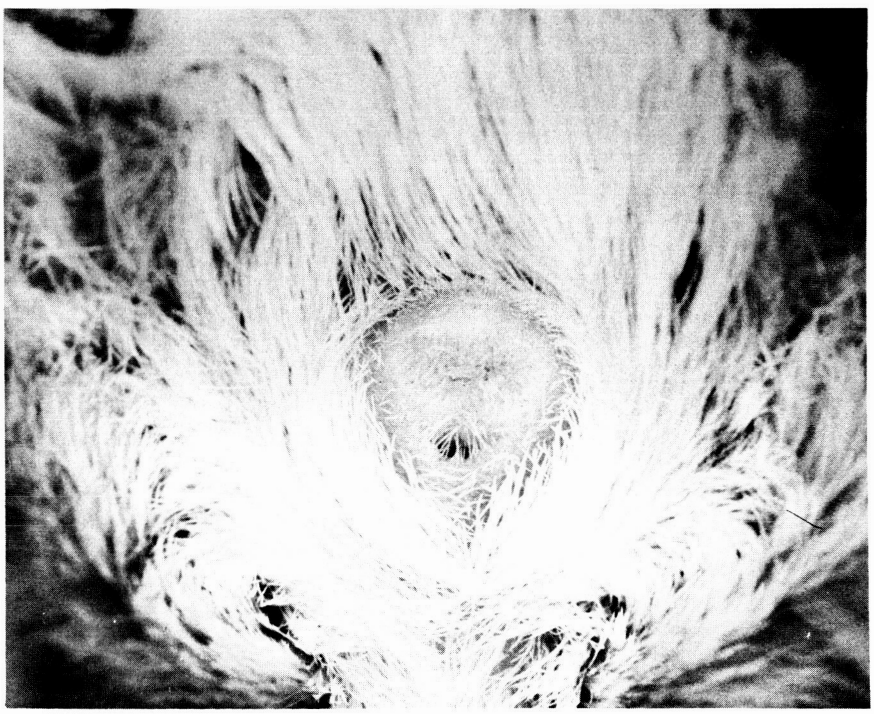
One of these cores was removed intact from an animal. It was reasonably solid, crenulated, elongate cone-shaped, with a bifurcated tip, which indicated that sloughing of the lining involved at least a portion of the uterine horns. It may be just coincidence that the animal from which this core was removed never has undergone another estrus period.

Reproductively Active Male

No males, either fresh from the field, hormone injected, or laboratory-maintained, have exhibited conspicuous scrotal testes as seen in the field. Eight laboratory-maintained animals have been observed with naturally enlarged testes that can be forced down into, and retained for several seconds in, a reasonably well developed scrotum.

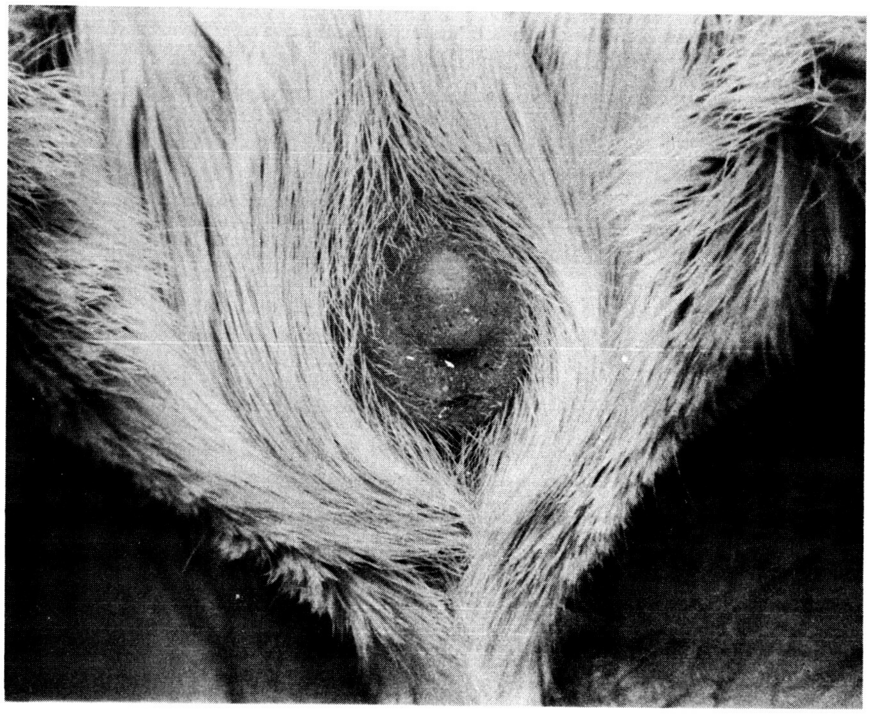


A. Anestrus

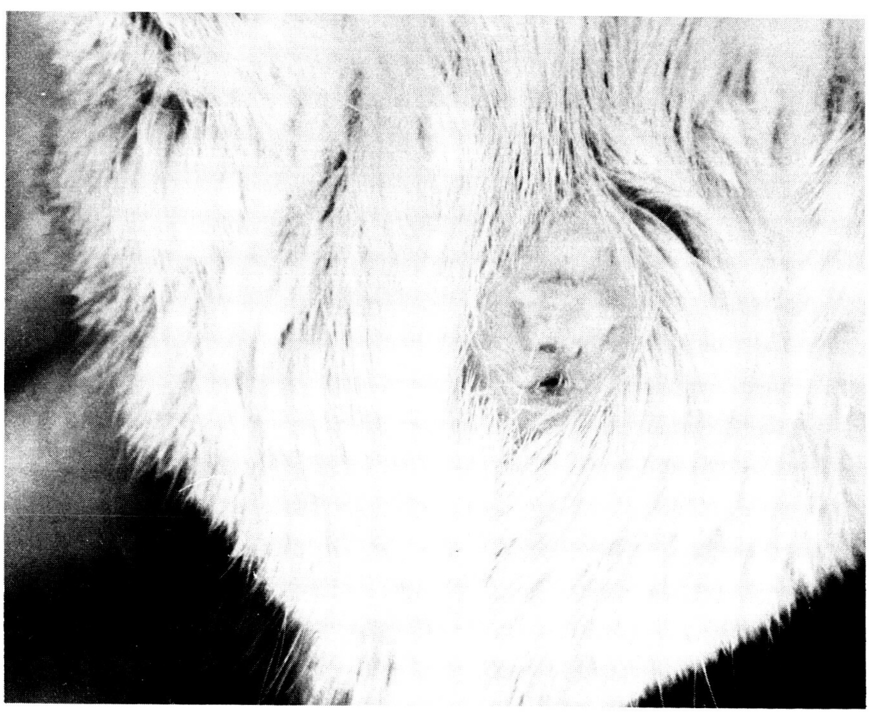


B. Proestrus

Plate I Genitalia of female Perognathus longimembris



A. Estrus



B. Metestrus

Plate II Genitalia of female <u>Perognathus longimembris</u>

Concomitant with testicular enlargement there is an increase in the amount of observable erectile tissue surrounding the os baculum, giving a rugose texture to the organ. In the inactive male, the penis is characteristically thin and pale with little vascularization.

Natural Reproductive Cycle

There is little doubt that the reproductive cycle of Perognathus in nature is correlated with the annual solar cycle, but subject to perturbations by local climatic conditions. Collection records of a number of authors show juvenile pocket mice appearing as early as March and as late as June. Chew and Butterworth (5) made observations on Perognathus and Dipodomys in their ecological study of rodents at Joshua Tree National Monument in California. They provide data showing that for the months of March, April and May, 70-100% of trapped Dipodomys merriami are reproductively active with at least 18 to 25% of these pregnant, and 40 to 60% lactating. They made only a few observations of reproductively active Perognathus in the same study, and simply note that all observations on pregnant Perognathus or of Perognathus with scrotal testes, and of very young animals, were in February, March and April.

French (8) notes that juvenile pocket mice appear in numbers in June at the Nevada Test Site, suggesting that they are probably born in April or May. Both authors note the lability of reproductive cycles in these desert rodents, attributing this to seasonal variation in rainfall, plant growth, and other ecological factors.

Laboratory Reproductive Cycles

At the beginning of the calendar year 1965, we had in our holding facility several hundred pocket mice (P. longimembris) which had been collected during the spring of 1964.

Two groups of P. longimembris were selected, each composed of 80 females and 20 males. One female group was intended strictly for observation, weights, and pairing of receptive females. The other female group was not weighed, and animals for hormone experimentation were taken from it. Both groups were maintained in close proximity in the holding facility and both received the same special diet*.

Observation of genitalia was initiated in mid-January and consisted of daily inspection and weighing of about 50 animals. In this way any one animal was seen every third day. Later this procedure was discarded in favor of daily observations of only those females that were known to be active. Checks of the entire group were made every 5 to 7 days and active animals were then inspected daily with the others.

In order to eliminate variation due to changes in gastrointestinal contents, all weighing was done between 0800 and 1000 hours on animals with empty cheek pouches.

Estrus has been noted in less than one-third of the 160 P. longimembris under observation. Animals exhibiting estrus are plotted in Figure 1 along the verticle axis in order of appearance of estrus. In a large number of cases, once estrus occurred the animal entered into a polyestrous period of variable time duration. This is noted in Figure 1 along the horizontal axis. In a few instances,only a single estrous cycle was noted.

The beginning of the polyestrous period for this species appears to be mid-January. However, less than 5% of the animals were reproductively active during January. By about mid-February reproductive activity showed a steady increase which continued throughout March at an increasing rate. There is evidence that the peak of reproductive activity for P. longimembris under conditions in this laboratory has not yet been reached.

The triangles in Figure 1 represent pairings of receptive females with active males. Pairing methods and results are discussed below.

* See Page 16

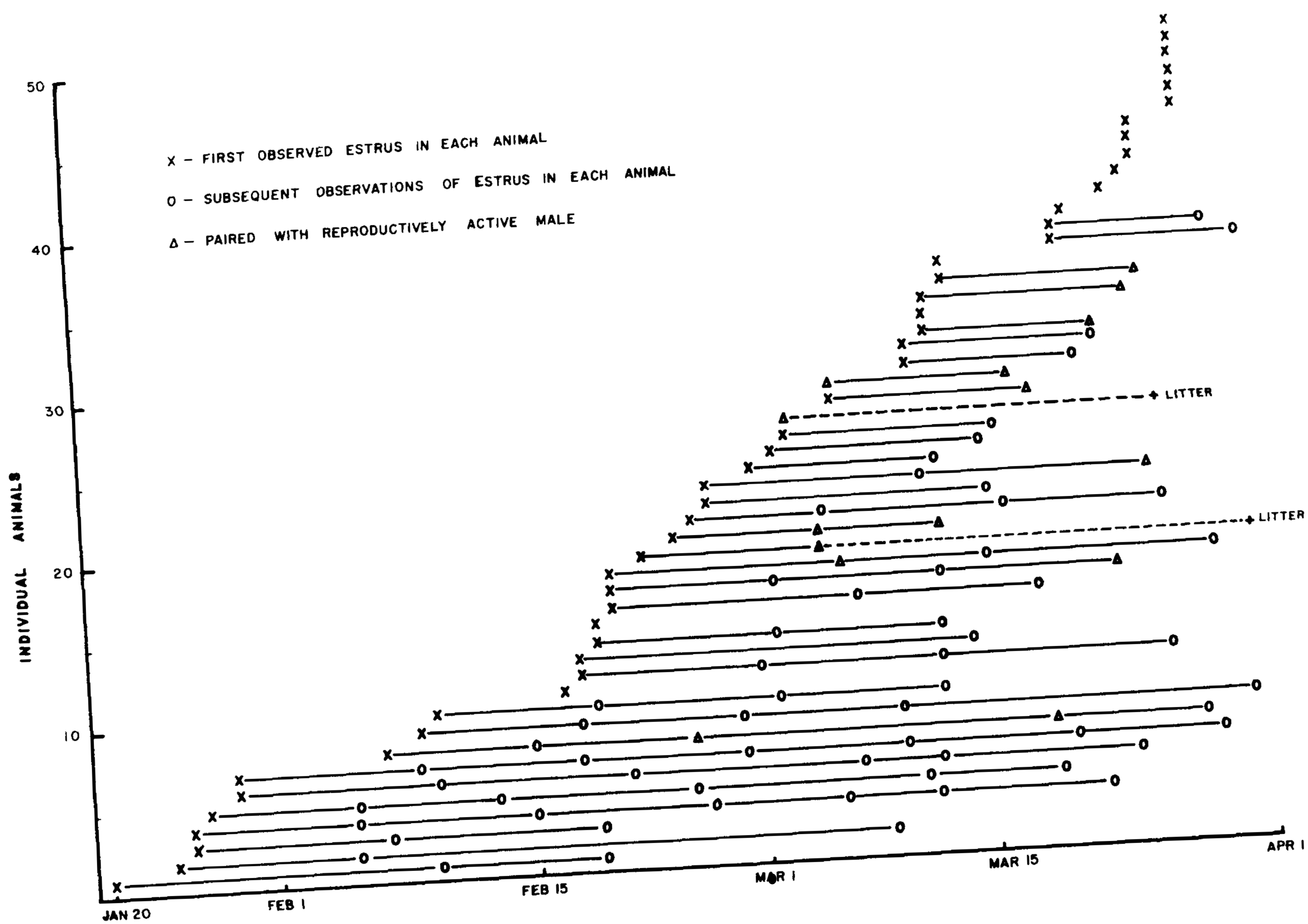


FIG. 1 – TIME OF APPEARANCE OF ESTRUS AND REPEATED ESTROUS CYCLES IN *PEROGNATHUS LONGIMEMBRIS*

Comparison of Field and Laboratory Animals

In his paper on reproduction in *Dipodomys m. merriami*, Chew concludes that success depends upon selection of females tolerant to captivity and able to maintain a body weight normal to wild animals (3). Underweight females in his laboratory did not undergo estrous.

Adult body weight of field animals (*P. longimembris*) in Chew's Mojave Desert study was 8.1 and 8.8 gms for the years 1957 and 1958 respectively (5). The mean weight of female animals received by this laboratory, but weighed several days after capture, from the same or nearby collecting site as Chew's is 8.6 gms (range 6.4 - 12.2 gms). The same animals approximately 9 months later weighed 9.4 gms (range 7.4 - 11.0 gms) indicating good adjustment to our laboratory conditions.

A group of males collected in the spring of 1964, and in our laboratory for approximately 9 months prior to the period of observation, were examined routinely for scrotal testes during the period from January to April. None were found. Examination of 38 *P. longimembris* coming in from the same site this season (1965) has revealed no overt "breeding condition" animals.

Judging from time of appearance of juveniles, copulations may take place as early as mid-January in the Mojave Desert habitat, and continue possibly through April. With limited manpower, the likelyhood of finding nesting females with young during this period is extremely remote, since pocket mouse density is estimated at approximately 1 per hectare (5). Nevertheless, on the expectation that a single "find" would add measureably to our understanding of pocket mouse ecology and breeding habit, an attempt was made to excavate *Perognathus* burrows in Whitewater (near Palm Springs) in the Mojave Desert, California.

It was possible to differentiate between *Dipodomys* and *Perognathus* by burrow size. Judging from burrow diameter, six burrow systems of *P. fallax* or *P. formosus* were found and excavated.

The burrow systems traced were relatively simple with only 2 to 5 branches (assuming none of the tunnels were lost in excavation). The depth of burrows was in general less than 6-8 inches, but one spiraled around the roots of a small bush and reached a depth of 18 inches.

No mice, nest chambers, or signs of food storage were encountered. One torpid lizard (genus: *Uta*) was found.

It is evident from comparative field and laboratory data that the breeding season for *Perognathus* is quite labile. Certainly knowledge of how to produce an active breeding colony of pocket mice in the laboratory would be greatly enhanced by more field observations. However, field observations are necessarily limited by the expense involved and small yield per unit effort.

Induced Breeding Cycles

Whether the start of the breeding cycle is extrinsically or intrinsically cued, there is little doubt that ovaries and testes become active in response to specific hormones. In a series of pilot experiments, estrogen and other estrogenic and androgenic hormones were used without success on *P. longimembris*. Within the last year, however, chorionic gonadotropin hormone (CGH) has become available and has proved to be an effective agent for stimulation of both ovarian and testicular activity in *Perognathus*.

The lyophilized CGH was dissolved and diluted with physiological saline to a strength of 2000 units/ml, and administered subdermally with a micrometer syringe.

A series of experiments undertaken to bracket the dose and dose rate of the hormone are summarized in Table 1.

Based on these estimates, a group of 10 anestrus females and 10 males were started on a 100 unit daily dose. By the 7th day, the external vaginal orifice was observed to be open in 6 animals and remained so from 2-5 days. The vaginal orifice of two animals were still sealed on the 16th day. None were in a condition that resembled natural estrus. Several pairings were tried, but none were receptive. Some of the hormone treated females remained extremely aggressive.

TABLE 1

Chorionic Gonadotropin Experiments

I. 200 Units, Twice a Week, 4♂, 4♀

All females open and moist on 7th day (3/4 on 6th day), but not swollen. One female slightly swollen on 11th day, but not in full estrus. All but one closed on 12th day.

Summary - No external sign of estrus.

II. 100 Units, Daily, 3♂, 4♀

Two females open, moist, very slightly swollen on 5th day. All females open on 7th day, but no complete estrus. One female in partial estrus on 9th day. All males responded to hormone with testicular enlargement by the 13-15th day. All females still open on the 15th day.

Summary - One partial estrus observed.

III. 100 Units Initially, Then 25 Units Daily, 6♀

Two-thirds females open 5th day, with three resealing on the 6th day. Two were noted to slough lining of vagina on 8th day. All were nearly regressed on 11th day. #1687 sacrificed - horns of uterus swollen, right ovary had several bloody spots.

Summary - No estrus observed, but lining of vagina sloughing noted. Histological pictures (Plate III, IV, V).

IV. 50 Units Daily and 25 Units Daily, 3♂, 3♀, 3♀

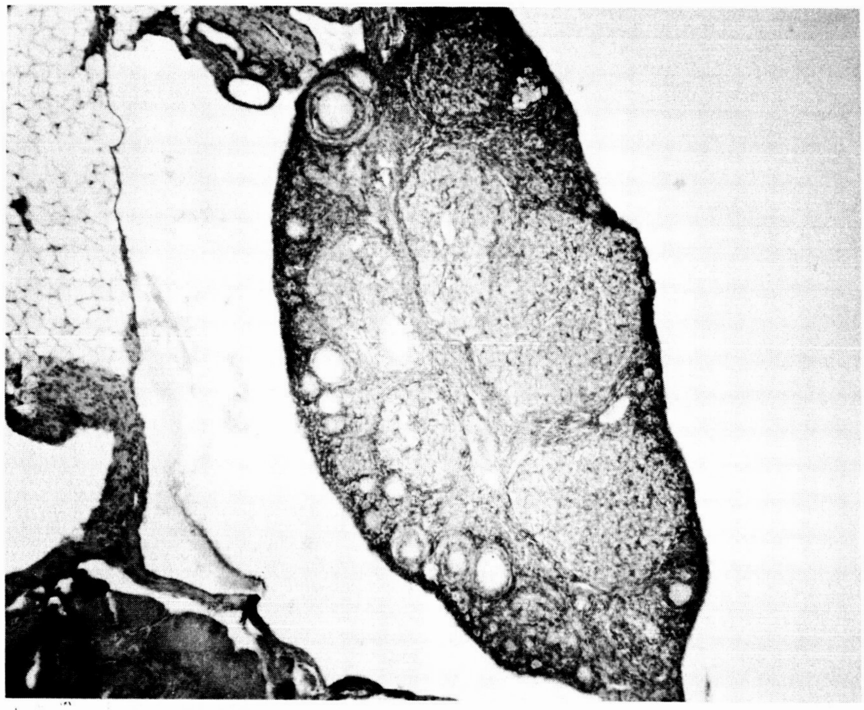
One female in 50 unit group - partial estrus on 1st day (not effect of hormone - natural estrus?). All females in both groups open, but not swollen on 5th day. All females in 25 unit group nearly regressed on 9th day, only one in 50 unit group partially open. Males slightly enlarged.

Summary - Response evident, but no estrus observed.

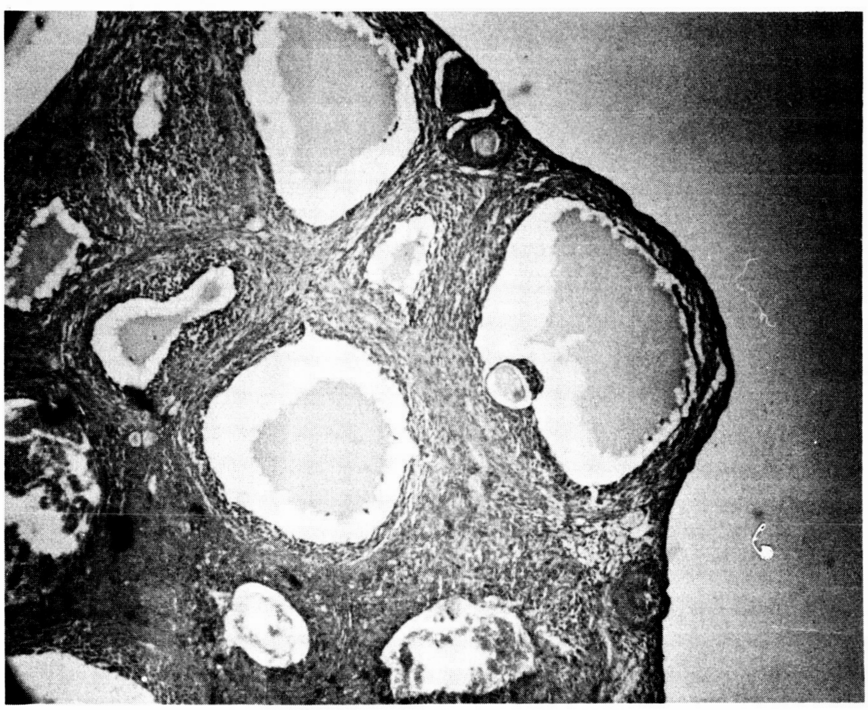
After a course of injection, several females exhibiting external signs of estrus were sacrificed. Histological sections of active ovaries and a control ovary are shown in Plates III, IV and V. Distended uteri and active ovaries were in evidence in all of the animals receiving hormones, whereas ovaries of control animals were small and quiescent.

The group that responded to CGH were given the course of treatment in October and November. A second group administered the identical course during the normal breeding season for Perognathus did not respond as well to the hormone. On the other hand, males appear to respond to the hormone irrespective of time of year it is administered.

Testes enlargement can be palpated in hormone treated, sexually active male Perognathus, but scrotal testes are rarely seen. Evidence that hormone enlarged testes contain viable sperm is provided by the fact that two successful pregnancies in this laboratory to date were with hormone treated males.

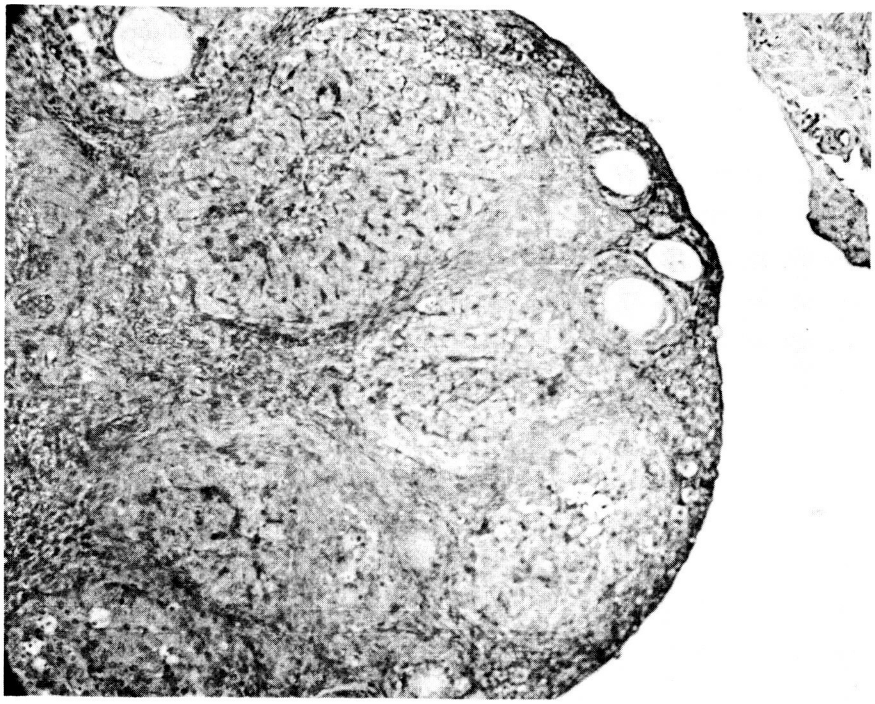


A. Normal - untreated animal in anestrus

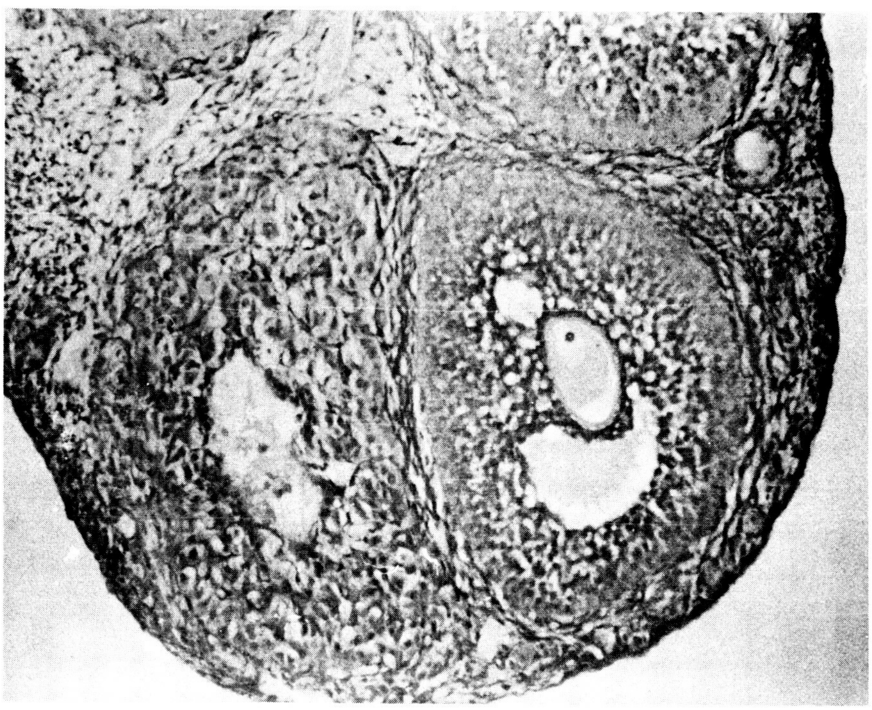


B. Active - hormone-treated animal shows externally visible signs of estrus when sacrificed

Plate III Ovaries of Perognathus longimembris - low power view



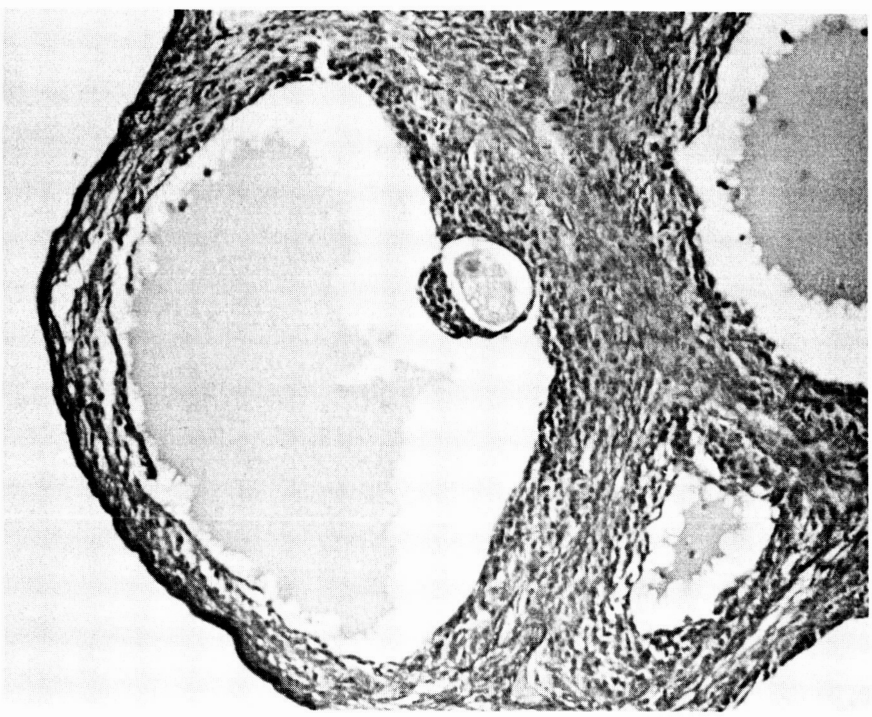
A. Normal - untreated animal showing atretic corpora lutea and inactive follicle



B. Active - hormone-treated animal showing growing Graafian follicle

Plate IV Ovaries of Perognathus longimembris - high power view

A. Active - hormone-treated - Graafian follicle



B. Active - hormone-treated - mature Graafian follicle

Plate V Ovaries of <u>Perognathus longimembris</u>

BREEDING AND REARING

Holding Facilities

Pocket mice are maintained in individual gallon-size, wide-mouth jars which contain two to three inches of sand. A mixture of grass seed, parakeet seed, rolled oats, and sunflower seed is made available *ad libitum*. No drinking water is required.

Temperature control in the laboratory is set at 22° $\pm$ 2°C. Relative humidity is maintained at 50 $\pm$ 5%.

Although the standard diet seemed to be adequate (based on sleek coats, bright eyes and activity), there was a question of whether it lacked a factor necessary for breeding. Judging from ecological factors, it was conjectured that water soluble vitamins might be scarce in the standard laboratory diet. The mouse normally has access to succulents in the field during the natural breeding season. Therefore, a new food mixture composed of equal parts hulled sunflower seeds, parakeet seed mix, rye, wheat, and rye grass seed soaked in water soluable vitamins (Avitron, T.M. pet vitamins) was given. Fresh field "grass" consisting of about equal parts monocots and dicots were given every other morning. The grass seed and fresh grass were avidly consumed. Ingestion of succulent materials by these animals greatly increased the amount of urine produced, although no overall gain in weight was noted.

The light period from 0600 to 1800 hours is normally provided by overhead flourescent fixtures. Therefore, light conditions in the laboratory are either uniformly dark or bright. The light regimen was altered to provide a small amount of light during the dark phase of the photoperiod. For this purpose, a partially darkened 7 w bulb night-light with opaque shield was placed to provide minimum night-time illumination.

Breeding

Two kinds of breeding cages were used: 15 gallon glass aquaria and a 4' x 4' wood and wire compartmented box. The 4' x 4' cage has 6 chambers built around one central chamber, with doors connecting the peripheral chambers with the central one. The theory is to allow animals to establish home territories in the 6 outer chambers and at the appropriate time let them come together in an unclaimed territory for mating. This method requires daily observations to establish the appropriate time to open the doors, and has the further disadvantage that no more than two animals can have access to the central chamber at any one time.

The simultaneous introduction of receptive pairs into the 15 gal. aquarium (288 sq. inches of floor space), with or without a temporary division, has been successfully employed and at present appears to be the better of the two methods.

A layer of desert sand 2-3 inches deep is placed in both types of chambers and seems to play a part in the pre- and post-copulatory behavior (1).

The method of selecting animals for pairing is very direct. Females judged to be receptive by external signs are placed with males with the largest palpable testes. They are observed for a short period, 15-20 minutes, to determine whether they are aggressive or pugnacious. Sometimes animals can be switched around to match "personalities", but this is seldom successful. If the male is pugnacious or reacts violently to the female, he is removed immediately. If the pair seem compatible, they are left together from 3-4 hours or sometimes overnight. The pair are then separated and the female placed in an isolation cage. These cages are larger than conventional holding cages and covered on three sides to reduce visual disturbance.

There have been seven (3♀, 4♂) fatalities in the pairings so far. In two cases the animals were found dead and partially cannibalized. In five cases death was not immediate. Subdued animals were always in a state of torpor, with bite wounds on the back and tail, and their sole response to touch was squeaking. They appeared to be in a state of shock and subsequently died.

The copulatory behavior of P. longimembris is sufficiently different from other species of Perognathus to warrant description (7). In one observed mating, the two animals approached one another directly after being placed in the breeding cage. After one nose to nose contact and a simultaneous leap, copulation ensued. The male mounted from the rear and both animals fell to the side. Copulation was accomplished in this position. The male did not bite or grasp with front feet, but grasped the female's tail with one of his hind feet and thrust rapidly. Mounts lasted no longer than 4-5 seconds and appeared to be terminated by the female. In a ten minute period there were from 20-25 mounts with an undetermined number of intromissions. During the final encounter the female bit the male on the head and a short kicking and scratching match ensued. The male ran to a corner and layed down, completely subdued. The female dug in the sand and preened herself. Twice the female approached the male and attempted to mount him, but he did not move. His only response was to squeak.

Inspection of the female immediately after copulation revealed her external genitalia to be regressed (estrus enlargement no longer visible) and the vaginal orifice sealed with a crust.

A total of 36 pairings have been made. In about half the trials the animals were either so aggressive that they were only left together for a short while, or a fatality occurred. In the remaining 18 pairings, only one copulation was observed; however, matings positively occurred in three instances. Two of these resulted in pregnancies. One litter of 4 and one litter of 6 was produced. One of the successful matings was with a male that had been treated with chorionic gonadotropin for 7 days followed by a lapse of 9 days without hormone, then a second period of 7 days with hormone. The other male had been injected with hormones for a period of 11 days before mating.

One of the bred females had been on hormone treatment 4 months earlier, but it is doubtful that this had a direct connection with the current success. The vaginal orifice of this female had been sealed for over a month prior to breeding. After pairing it was judged that the mating had not been successful as the female appeared to be in the normal state of regression with a hard core. It is evident that subsequent daily inspections of genitalia were not sufficiently traumatic to cause resorption of the embryos. The second successfully bred female was noted to have a larger than normal core after being with the male and was moved to an isolated chamber to wait for parturition. The gestation period was 23 and 24 days respectively.

Rearing and Breeding Young

Records over the past three years in this laboratory indicate that only a very small percentage (less than 1%) of the females received from the field during breeding season are pregnant. Since most animals received by us are collected in April, May and June from sites in the Mojave Desert, there is a possibility that the breeding season is beginning to decline by this time (5).

Various other reasons have been offered to explain this apparent low incidence of trapped pregnant *Perognathus*. Some suggest that fetuses of disturbed wild rodents are rapidly resorbed. Other guesses include the possibility that pregnant females are more wary of traps, or perhaps forage less, remaining closer to their home range and thereby avoiding trap lines. It is clear that a greater knowledge of the breeding cycle in nature is required before a totally acceptable explanation for this phenomenon can be generated.

Of the small number of pregnant pocket mice received in this laboratory over the past three years, several have produced viable litters. New-born *Perognathus* resemble any new-born rodent (Plate VI). Four litters born here were eventually reared to adults. The following is a description of the postnatal behavior of one *P. formosus* and the development of her litter (Plates VII and VIII).

On April 23, 1964, a small, grey juvenile *P. formosus*, weighing 21.6 grams, was received from Whitewater Canyon, California. The abdomen was enlarged, suggesting it was gravid. On April 27, a litter of 3 was delivered. Total body length was estimated at 3 cm. The dam nursed well and appeared undisturbed by the unnatural environment. In addition to her standard seed diet, she was fed carrots, lettuce, and bermuda grass during lactation.

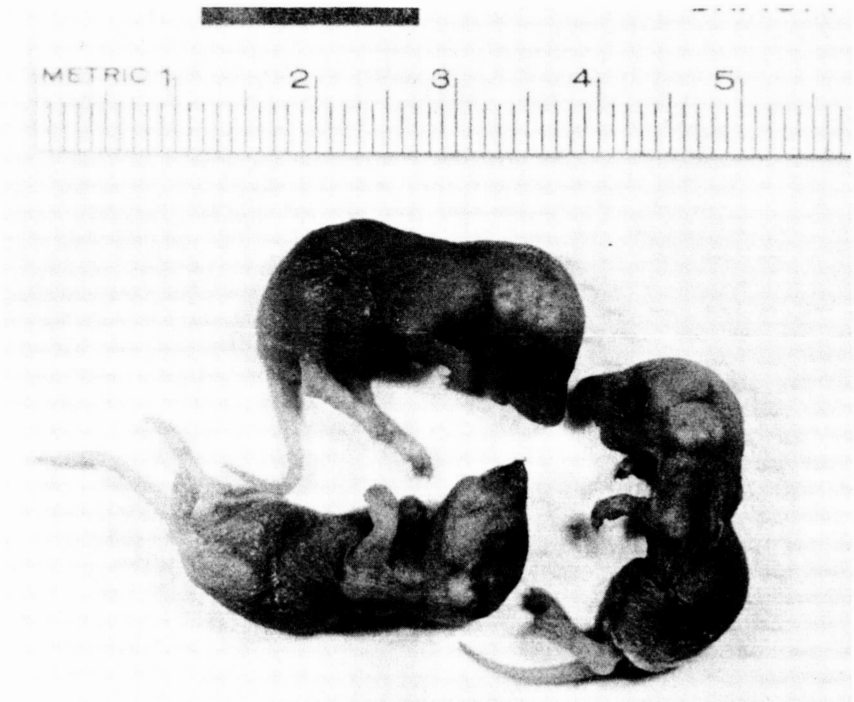


Plate VI *P. longimembris* litter; 2 days

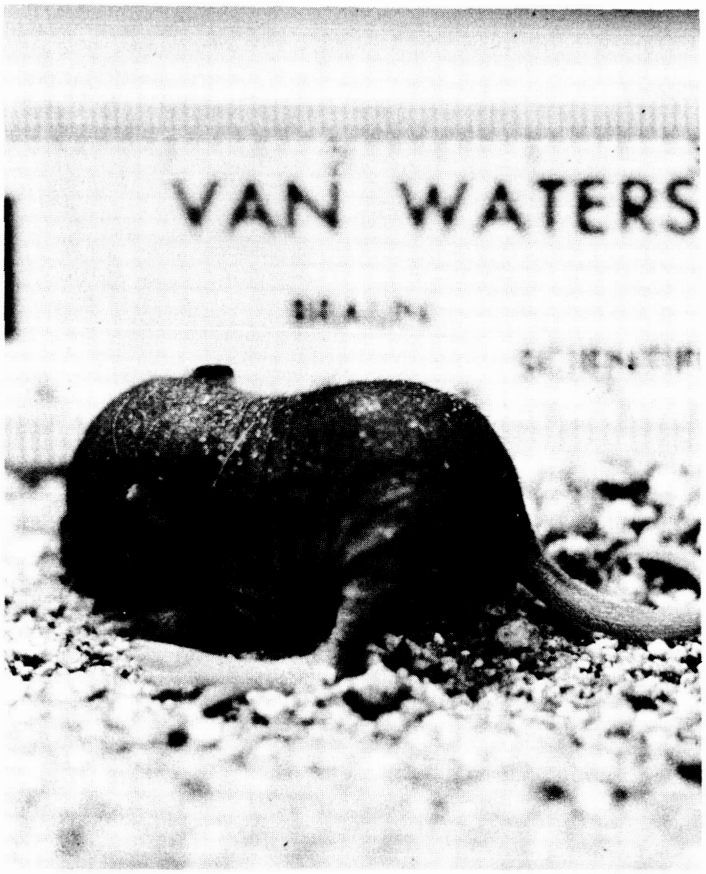


Plate VII P. formosus; 11 days

Plate VIII P. formosus; 16 days

At 7 days, the young were measured and weighed. Body length was 3 cm; tail length 1 cm; body weight 3.5 gms. Eyes and ears were still unopened. They were able to crawl about in the sandy substrate of the cage.

At 11 days, body length was 6.5 cm; tail length 2.9 cm; body weight 4.9 gms. Their coats were forming and one animal was observed eating a piece of carrot.

At 14 days, their eyes were open. They were active in the cage, moving about and causing the dam much consternation as she tried to keep them together. Their body weights ranged from 6.7 to 7.5 gms. Body length was 5.0 cm; tail length 3.5 cm. Their coats were becoming denser. Lettuce and cabbage formed part of their diet.

At 18 days, they were very independent. They carried seeds in their cheek pouches and had the run of the cage. The dam no longer attempted to keep them together. Body weights ranged from 7.9 to 9.0; body length 5.2 to 5.5 cm; and tail length 3.7 to 3.9 cm.

At 31 days, their body weights were between 11.5 and 11.9 gms. They appear fully developed in all respects except size. At 38 days, they were separated from the dam. The dam still had a grey juvenile pelt and was difficult to differentiate from her litter.

In late spring, four pregnant P. longimembris were received from the field and delivered litters in the laboratory. They are tabulated as follows.

Dam	Born	No. of Young	
L-1690	5-4-64	3♀	1♂
L-1296	5-7-64	2♀	1♂
L-1301	5-12-64		2♂
L-1292	5-14-64	3 (?)	died shortly after birth

By June 26, 1964, the surviving 9 animals had achieved approximately full growth, having a mean weight of 7.4 grams (range 6.4 to 8.2 gms).

On this date one male from L-1301 was placed with L-1690 litter. The other male from L-1301 was placed with the L-1296 litter. Three days later, the first male was found dead, showing signs of having been attacked by the others. Subsequently, all the males and two females were killed, leaving three females who lived together for six months in a 15 gallon aquarium. During this period there was considerable fighting, but no deaths.

Beginning in January of 1965, these remaining female litter-mates were separated and observed regularly for reproductive activity. No signs of estrus have been seen to date (April 1, 1965).

CONCLUSIONS

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It has been demonstrated that it is possible to breed Perognathus longimembris in captivity. It is evident that the yield per unit effort is quite low at the present state-of-the-art; however, several courses are open to improve the situation. For example, a renewed effort to obtain breeding in litter mates is indicated. The fact that litter mates have been kept together for long periods without mortality suggests their antagonistic behavior patterns may be altered. With new knowledge of how to predict receptivity in females and to produce sexually active males, this approach may be successful.

Routine observations of reproductive activity in laboratory-maintained animals must certainly continue, and a greater effort should be made to increase the incidence of reproductively active animals. Diet, light, and temperature are among the parameters that will be studied further for their role in initiating and maintaining reproductive activity in captive and laboratory-reared animals.

author

SUMMARY

Work to date in this laboratory has provided data on the initiation, incidence, and length of the estrous cycle in Perognathus longimembris. Two litters have resulted from laboratory-induced matings and a gestation period of 23 to 24 days for this species has been determined. Laboratory and field data have corroborated observations of others that the breeding season of Perognathus is quite labile and may extend from January through May or June, depending upon local conditions.

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GLOSSARY

Anestrus - A lengthened period of seasonal inactivity intervening between two estrous cycles.

Diestrus - A period of sexual quiescence separating recurring metestrus and proestrus periods.

Estrus - A periodic attainment of hormonic balance resulting in a period of sexual receptivity or "heat".

Estrous Cycle - The progressive accomplishment of the anatomic, physiologic and psychologic alterations characteristic of the periods of proestrus, estrus, metestrus and diestrus.

Metestrus - A short period of subsiding follicular function following estrus.

Monestrous - Completion of a single estrous cycle annually, the cycle occuring at a rather definite season.

Polyestrous - Completion of two or many estrous cycles each year, if not interrupted by pregnancy. The recurring cycles may be limited to only a part of the year or may occur uninterruptedly throughout the entire year.

Proestrus - A period of heightened activity of the ovarian follicles preceding estrus.